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MORPHOMETRIC PLASTICITY IN *PRIONCHULUS PUNCTATUS* (COBB, 1917) ANDRÁSSY, 1958 AND *CLARKUS PAPILLATUS* (BASTIAN, 1865) JAIRAJPURI, 1970 (NEMATODA: MONONCHIDA): ADAPTATION TO DIFFERENT HUMUS FORMS?

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Abstract.— Morphometric variability was studied in *Prionchulus punctatus* and *Clarkus papillatus* from closely related forest sites: Site 1 (eutrophic to calcic mull humus), site 2 (contiguous to site 1, eutrophic mull humus with a more or less leached soil), site 3 (acid mull humus), site 4 (located in site 3 but just under the crown of an old oak, moder humus), site 7 (moder humus, developed in a wide area). Results from correspondence analysis for both nematode species from site 2 suggested two distinct population types (a) with small individuals (Pp: 1.85 ± 0.05 mm and 87.2 ± 5.7 μm for body length and tail length respectively; Cp: 1.11 ± 0.02 mm and 78.5 ± 1.9 μm) with typical characteristics of populations collected from a calcic mull and (b) larger individuals (Pp: 2.14 ± 0.04 mm and 100.2 ± 1.8 μm for body length and tail length respectively; Cp: 1.21 ± 0.01 mm and 83.3 ± 2.2 μm) similar to populations collected from an eutrophic mull. Results from correspondence analysis from site 4 showed that the populations of the two species had intermediate characteristics between populations collected from a mull humus and from a moder humus. Moreover, a laboratory culturing experiment with adult *Clarkus papillatus* collected from site 3 and cultured on three humus forms (calcic mull, site 1; acid mull, site 3; moder, site 7) showed that this species reproduced successfully on mull acid only. The conjunctural or the structural influence on morphometric plasticity of these species is discussed from a functional ecology aspect.

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Key words.— Humus forms, Mononchida, Morphometric plasticity, Nematoda.

INTRODUCTION

Intraspecific variability analysis was the object of several works proving that morphological characters varied within individuals of a same species. These variations which affect all the nematode groups were more particularly studied in plant parasitic nematodes, such as Tylenchida (Doucet et al. 1996; Geraert and Crappe 1981; Goodey 1952; Netscher and Pernes 1971; Popovici 1988; Singh et al. 1985; Subbotin et al. 1999; Wu 1960; Yeates 1978) or Dorylaimida (Brown 1985; Brown and Topham 1985). Work was also carried out on free living nematodes, such as Mononchida (Ahmad and Jairajpuri 1981; Arpin and Ponge 1984; Arpin et al. 1988; Coomans and Lima 1965), Cephalobida (Boström and Gydemo 1983; Boström 1988; Sohlenius 1988), Dorylaimida (Ferris 1983), Diplogasterida (Geraert 1983), or zooparasitic forms (Tomalak 1994). The study of the morphological and morphometric plasticity has great importance in nematology as it covers diverse inter-connected field research: speciation problems, phylogenetic analysis, biogeography, in relation to hosts/parasitic forms/pathogenesis, adaptations to environmental conditions, functional ecosystem processes.

Nematode systematics and the phylogenetic approach evolved considerably over the last years, benefiting from the use of biochemical, molecular and genetic complementary approach methods (Lorenzen 1996; Powers and Fleming 1998). However, the need remains for the definition of the limits of the variability of different morphometric and allometric characters and their diagnostic importance at a species level, based on the comparison of populations either from different geographical or environmental conditions or from a same site.

In addition, the current development of studies on biodiversity and the durable management of ecosystems require precise nematode determination and limits of intraspecific variability, as several recent works, reviewed in particular by Wasilewska (1997), considered that the nematode fauna (either as a whole; trophic groups; species level or species groups) are key to environmental processes. Thus, species plasticity may not only reflect the ability of the nematode to adapt to various biotopes or environmental changes (such as global change) but could also be associated with functional processes (changes in morphology could be linked to trophic modifications, then to the impact of a species in the ecosystem; explanation of the coexistence of species, Yeates 1986, 1987a; Yeates and Wardle 1996). Hence, it is important to know what extent the variability of characters can be related to conjunctural or structural influence.

From this ecological aspect, the Mononchida nematode populations appear to be excellent indicators of the nature and the evolution of forest humus (Arpin 1979; Arpin 1991). Analysis of ubiquitous parthenogenetic species such as *Prionchulus punctatus* (Cobb, 1917) Andrássy, 1958 or *Clarkus papillatus* (Bastian, 1865) Jairajpuri, 1970 have shown that in relatively homogeneous sites, humus form was the most important factor influencing the distribution and the morphology of both species (Arpin and Ponge 1984; Arpin et al. 1988). Previous studies noted that other factors, such as soil water content or rainfall, pH, organic matter content or changes in associated vegetation (e. g Boag 1974; Boag et al. 1992; Brzeski 1995; Háněl 1996; Jimenez Guirado et al. 1993; Winiszewska-Ślipińska and Skwiercz 1987; Yeates 1987b) also had effects on Mononchida populations. A previous study on *C. papillatus* showed that site heterogeneity resulting from natural forest dynamics via changes in humus dynamics influenced the morphometric variability of *C. papillatus* and the distribution of Mononchida (Arpin and Armendáriz 1996). A previous study which analysed four different humus forms separated only by short distances in the same forest, showed that a population of *P. punctatus* collected from a moder humus form developed in a zone with an acid mull humus form appeared to have intermediate morphological characters, thus illustrating the duality of the influence of environmental conditions (Arpin et al. 1984). This paper aims at determining whether the same effect would be observed in other particular sites (for example, mosaic calcic mull humus and eutrophic mull humus) as well as comparing the morphometric variability of *C. papillatus* from the same sites. What implication could these results have with regard to the ecological aspect? The choice to study these two species was dictated by the existence of previous works on their morphometric variability from these very experimental sites and their presence in all the different humus forms, contrary to other species such as *Anatonchus tridentatus* or *Mylonchulus brachyuris* which are only present on mull humus.

MATERIAL AND METHODS

Experimental sites

A description of the experimental sites is presented in Arpin et al. (1984). Briefly, this work was carried out in an oak grove within the Sénart forest near Paris (France, 48°40' latitude N and 2°26' longitude E) [*Quercus petraea* (Mattus.) Lieb. and *Quercus robur* L.]. Sites 1–4 were located approximately 30 meters from each other, on a gentle gradient sloping towards the Seine valley. In contrast, site 7 was located approximately 900 meters from sites 1–4, on the plateau zone.

Site 1 had a silty-clay soil with in-depth calcareous substrate. Vegetation comprised a coppice of *Fraxinus excelsior* L. with standards of *Quercus robur* L., and a herbaceous layer dominated by *Hedera helix* L. and *Mercurialis perennis* L. The humus form was an eutrophic mull, but occasionally calcic mull humus can be encoutered when the limestone rose to the soil surface. Site 2 was contiguous to site 1, with a silty soil and a coppice of *Tilia cordata* Mill. with standards of *Quercus robur* L., and a herbaceous layer dominated by *Mercurialis perennis* L. and *Euphorbia amygdaloides* L. The humus form was similar to the eutrophic mull of site 1, but the soil differed from the former due to a clear leaching and the burrowing activity of moles. Sites 3 and 4 supported a sessile oak grove (*Quercus petraea* (Mattus.) Lieb.) with a coppice of lime and a herbaceous layer dominated by *Rubus fructuosus* L. The humus of site 3 was an acid mull form. Site 4 was located within site 3, but under the crown of an old oak and had a morphologically moder humus form. Consequently, it was necessary to compare the Mononchida populations with those collected from a standard moder humus form developed on a larger scale, i. e site 7. Site 7 supported a sessile oak grove with sparce *Pinus silvestris* L. and *Betula verrucosa* Ehrh., the herbaceous layer dominated by *Pteridium aquilinum* (L.) Khun.

Analyses

Adult Mononchida were collected by the washing and sieving soil method (Dalmasso 1966 modified by Arpin 1979), fixed and processed in anhydrous glycerin (Seinhorst 1959), then measured under microscope. Numbers of female *Prionchulus punctatus* and *Clarkus papillatus* extracted from the experimental sites varied, site 1 (Pp = 7, Cp = 22), site 2 (40, 41), site 3 (13, 75), site 4 (40, 365) and site 7 (23, 94).

Data was analyzed using correspondence analysis (FCA) (Greenacre 1984). To facilitate the interpretation of the graphs, the morphometric variates (body, oesophagous length, tail length, body width, position of the vulva, buccal cavity length, buccal cavity width, apex of the dorsal tooth, A, B and C ratios were coded as follows: L, OESO, T, W, VULVA, BCL, BCW, Apex, A, B, C) and were analysed after focussing and reweighting of the data. Each variate x was transformed into $x' = (x-m) / s+10$, m being the mean and s the standard deviation. By this way, still suggested by Greenacre (1984) all variates have the same contribution to the axes. This gives to correspondence analysis (FCA) similar properties to principal components analysis (PCA) except that the simultaneous projection of variates and individuals is authorized on factorial axes. In addition, all variates were duplicated, the original variate indicating higher values for a given measurement and a new variate (complementation to 20) indicating lower values, the two points projected visualizing a gradation from lower to higher values (Arpin and Ponge 1984; Arpin et al. 1988; Arpin and Armendáriz 1996).

Culturing *Clarkus papillatus*

In order to test to what extent the morphometric values observed in *C. papillatus* from the different humus forms could represent an adaptation to the environmental conditions, an experiment in controlled conditions (temperature, soil moisture, food supply) was initially carried out. Soil samples obtained from sites 1 (calcic mull), 3 (acid mull) and 7 (moder) were sieved (0.5 mm diameter) then sterilized (drying at 105°C during 48 hours). Watered soils (pF = 2.5) with soil solutions extracted by centrifugation (5000 g during 10 minutes) were placed into 10 cm diam. Petri dishes. *Rhabditis* sp. cultured on Nigon's medium (Nigon 1949) were added as prey species. Approximately 10 days later, 30 females of *C. papillatus* collected from site 3 (acid mull humus) were introduced into each Petri-dish with 5 replicates of each humus form. After 5 months (April to September 1997) *C. papillatus* females were collected from each humus plot and measured.

RESULTS

Study of *Prionchulus punctatus*

Correspondence analysis of data from all five study sites accounted for 71% of the total variance (Fig. 1A). The data suggests the existence of two distinct morphological populations from site 2, comprising small and large individuals (with reference to body, tail and buccal cavity length and width). Individuals collected from the contigous site 1 were closely related to the larger specimens collected from site 2 (Fig. 1B). Table 1 summarizes the measurements of the discriminating characters of each population.

Similarly, results from FCA (Fig. 1A) also showed that the population collected from site 4 was intermediate to populations from sites 3 and 7. This fact was emphasized when comparing the average points of each population from each site (Fig. 1B). Graphing tail length versus body length (Fig. 2A) and length versus width of the buccal cavity (Fig. 2B) suggested that the site 4 population had some characteristics related to individuals collected from site 2 (mull humus form) and to those collected from site 7 (moder humus): with regard to buccal cavity size, individuals from site 4 were closely related to those collected from site 2; in contrast, with respect to body and tail length, they were closer to those collected from site 7.

Study of *Clarkus papillatus*

Field study. Correspondence analysis of data from sites 1 and 2 accounts for 51.3% of the total variance [Figs 3A (individuals) and 3B (variates) are separated to facilitate the interpretation of the analysis only]. The data suggests the existence of two distinct morphological populations from site 2 comprising relatively large size individuals (positive values of axis 1, with reference to body length and width and tail length) and small size individuals which have some affinities with the majority of individuals collected from site 1 (negative values of axis 1). Graphing tail length versus body length (Fig. 4A) and buccal cavity width versus buccal cavity length (Fig. 4B) illustrates this fact: if the buccal cavity measurements of the three populations showed some overlapping statistically, a clear separation occured when we considered the body and the tail size.

Correspondence analysis of data from sites 3, 4 and 7 accounts for 50.7% of the total variance (Figs 5A and 5B). The data suggests that the individuals from sites 3 and 4 seemed relatively grouped and may be separated from those collected from site 7 (large individuals, positive values of axis 1). However, if we consider the graphs in figure 4, we

	Site 1 (n=7)	Site 2 small animals (n=13)	Site 2 large animals (n=27)	Site 3 (n=13)	Site 4 (n=40)	Site 7 (n=23)
Length (mm)	2.01±0.13	1.85±0.05	2.14±0.04	2.21±0.06	2.13±0.05	2.07±0.07
Tail (mm)	103.6±5.6	87.2±5.7	100.2±1.8	140.5±9.8	130.9±3.1	132.9±3.7
Buc. cav. length (mm)	39.8±1.1	39.1±0.6	39.4±0.4	39.0±0.7	39.8±0.3	39.5±0.5
Buc. cav. width (mm)	22.6±0.7	22.7±0.5	22.5±0.2	22.6±0.4	23.0±0.2	24.0±0.5

Table 1. Means with confidence interval ± $t_{0.05}$ S_x of selected discriminant characters of *Prionchulus punctatus* according to the different sites used for the FCA.

	Acid mull culture (n=60)	Clacic mull culture (n=2)	Moder culture (n=2)
Length (mm)	1.18±0.02	(1.15–1.06)	(1.15–1.14)
Tail (mm)	71.7±1.4	(66.3–65.9)	(75.2–70.0)
Buc. cav. length (mm)	25.4±0.5	(27.7–22.1)	(26.0–26.7)
Buc. cav. width (mm)	14.5±0.3	(16.3–11.7)	(15.0–14.5)

Table 2. Measurements of some discriminant characters of *Clarkus papillatus* in culturing experiment.

notice that, in respect to their body and tail length, the site 4 individuals are closely related to those collected from site 3 (mull humus) whereas their buccal cavity size more closely related them to those collected from site 7 (moder humus).

Culturing experiment. After five months, 650 individuals were collected on Petri dishes filled with the acid mull humus from site 3 (210 females and 440 larvae) but only 4 individuals (2 females and 2 larvae) on the calcic mull humus from site 1 and 5 individuals on the moder humus from site 7 (2 females and 3 larvae). Table 2 gives the measurements of some variates for the individuals collected from each humus form. Although this data cannot be easily used, it should be noted however, that *C. papillatus* individuals reared on acid mull humus, had a slightly smaller tail length than the field ones.

DISCUSSION

The humus form is the most important factor influencing the distribution of the Mononchida nematodes and the morphology of both ubiquitous parthenogenetic species *P. punctatus* and *C. papillatus* (Arpin 1991). However, the above results, based on closely related forest sites, emphasized certain interesting aspects.

Firstly, correspondence analysis of data for both species showed a gradation in the morphology of animals according to humus forms and confirming previous studies on Mononchida (Arpin and Ponge 1984; Arpin et al. 1988; Arpin 1991; Arpin and Armendáriz 1996). Generally, the calcic to eutrophic mull humus (sites 1 or 2) is characterized by small size animals (body length, tail length and buccal cavity length or width); the acid mull humus (site 3) as well as the moder humus (site 7) are characterized by larger animals. This gradation in measurements agreed with previous observations on *P. punctatus* (Arpin and Ponge 1984) and *C. papillatus* (Arpin et al. 1988).

Secondly, at site 2, as well in *P. punctatus* as in *C. papillatus*, it was possible to distinguish two types of populations. Small individuals seemed to show morphometric affinities with those collected from site 1 (clearly evident in *C. papillatus*), while larger individuals appeared to be closely related to individuals obtained from site 3. This is possibly due to the intermediate situation of site 2, near sites 1 and 3, which offered calcic and eutrophic (or acid) mull humus in patches Changes in composition of Mononchida communities have been previously related to the mull character with calcic deposits on site 1 and the tendency to leaching and acidification of the mull on site 2 (Arpin et al. 1984). We could thus hypothesize that each population retained the morphometric characters of the original populations from each humus form. In other words, the morphological types previously described for these two species (Arpin and Ponge 1984; Arpin et al. 1988) could reflect an adaptation to environmental conditions. Results from the culturing experiment could confirm this, as only acid mull humus allowed an abundant development of *C. papillatus*. However, this result should be treated with caution. The accumulation of toxic products such as organic acids or polyphenols in the Petri-dish moder humus experiment is one possible reason of the negative result. The unexpected negative result on the calcic mull treatment, a known suitable environment for *C. papillatus*, is accurently unexplainable and may suggest problems in the execution of the experiment.

Thirdly, at site 4, we also noted a similar trend in both *P. punctatus* and *C. papillatus* which seemed to have uniform populations but where morphometric variates appeared intermediate between populations collected from an acid mull humus and a moder humus. Arpin et al. (1984) emphasized the particular character of this site. Morphologically closely related to moder, the similarity to moder humus of site 7 particularly concerned the litter which was affected at both sites by a weak humification rate, but still maintained good contact with mineral elements on site 4 (higher content of insolubilisation humin). On the contrary, with a better biological incorporation (in particular, higher organic matter content), the organo-mineral horizon A1 at site 4 had an organic matter composition closely related to that of the acid mull of site 3. Although, we recorded a higher acid pH and C/N on site 4 than on site 3. The study of the Mononchida species groups also reflected the duality of this site (originally mull, acid evolution). In other words, the morphometric analysis of both species, taking into account the particular characteristics of site 4, seemed to indicate the importance of environmental conditions on the morphometry of species, the populations showing gradual adaptations according to the changing physico-chemical characteristics of the humus.

It is difficult to explain the difference in results from sites 1 and 2 (separation of populations) and from site 4 (intermediate morphological characters). It is unlikely that this difference could be linked to the different abundance of individuals collected from site 2 as compared to site 4, results being similar in both species, but this finding requires further field research. From our data, it is possible to suggest that two sets of humus forms predominate, mull and moder humus, each one the result of the activity of specific major functional groups (Ponge et al. 1997; Ponge et al. 1998; Ponge 1999). Other types of humus represent intermediate forms, in particular the acid mull humus where morphometric variability, notably in *C. papillatus*, was always the most variable (Arpin et al. 1988). In these transitory humus forms, animals may show gradual adaptations which could be expressed in an irreversible process, beyond a certain chemical composition of the environment: for example, calcium content in mull and the content of organic acids or phenolic compounds in moder could be influential.

Previous studies of Mononchida have suggested that these nematodes are related to environmental conditions. Winiszewska-Ślipińska and Skwiercz (1987) showed that the distribution of Mononchida species in arable soils and natural peat biotopes in Poland were related to pH and organic matter content. Similarly, Jimenez Guirado et al. (1993) associated the distribution of Spanish mononchids species with a broader concept of habitat based on plant associations, although the interrelationship of soil and vegetation was also noted as being possibly influential. Háněl (1996) also reported the possible role of humus acid substances in the decrease of the abundance of Mononchida influenced by the age of spruce trees. Moreover, Arpin and Armendáriz (1996) illustrated the influence of natural forest dynamics, via humus form, on the nematode fauna and particularly on species of Mononchida in a zone with an acid mull humus in the beech grove biological reserve (La tillaie) of the Fontainebleau forest.

Humus forms may also influence the whole soil nematode fauna, not just Mononchida. In a recent work on the effects of global warming on nematode diversity in a Swedish tundra, Sohlenius and Boström (1999) reported that a climatic change had no rapid influence on the composition of the fauna, but that soil structure and vegetation seemed to have a stronger influence (mainly acid soils, but some sites were open grass-lands or agricultural areas). Moreover, Katajisto et al. (1999) investigating the influence of primary production on the soil faunal community in microcosms with a moder humus form, showed that during the experimental period, no treatment effects were found in the abundance or the biomass of functional groups of animals. Moreover, high organic matter content and also long-time lag in the system response were considered the main reasons for the small difference observed. Similarly, experimental modifications of litter supplies in forest soil on nematode species richness and community composition, suggested that, in a mull calcic humus, no alterations were found at the end of the experiment in the specific composition or the structure of the nematode population (Arpin et al. 1985). However, in an acid mull humus, in contrast to macrofauna and mesofauna (David et al. 1991; Ponge et al. 1993), a decrease in nematode abundance was noted at the end of the experiment (Arpin et al. 1995), although the same trends found in calcic mull could be observed at the beginning of the experiment. Moreover, effects of litter doubling on this acid mull humus were expressed by changes of the nematode fauna simulating an acidification of the environment. Wasilewska's overview (1997) suggested that soil nematodes could be used for characterizing ecological processes in soil. The morphometric data reported here suggest that ubiquitous species of Mononchida have the potential to indicate a particular functioning of the humus: the existence or the perenniality of well-established opposed forms (mull humus, moder humus) and the gradual modification of intermediate forms.

The apparent relationship between humus forms and Mononchida morphometrics is perhaps analogous to that described between plant-parasitic nematodes and their hosts. Previous studies reported significant morphometric differences between various natural and cultured *Xiphinema diversicaudatum* populations (Brown and Topham 1985; Brown 1985) and such differences were still apparent after four years of being cultured in a glasshouse under similar conditions. Authors concluded that geographical location was not likely to be the only factor which determined the morphometrics of a population, and the variability between the morphometrics of populations probably reflected the ability of the nematodes to adapt to various biotopes. Results by Singh et al. (1985) using *Meloidogyne incognita* cultured from a single egg-mass population on different plant hosts, underlined that body length variability was induced by the hosts and clearly varied more than genetically determined stylet length. Although a seasonal variability in body and tail length in relation to soil moisture and food supply was detected in *C. papillatus* (Arpin et al. 1988; Saur and Arpin 1988), it is less of an influence compared to the variability due to humus form as opposed to host effects on *X. diversicaudatum* or *M. incognita*. Doucet et al. (1996) noted that six isolates of *Pratylenchus vulnus* had significant intraspecific variability in relation to both their geographical origin and plant host, however, the existence of different pathotypes on the same host may have complicated the results. The coexistence of two morphometric groups in both Mononchida species from site 2 could reflect a similar process. Similar observations have been reported by Yeates (1978) on *Hemicycliophora chathami* where a giant and a "normal" forms cohabited in different soils in New Zealand.

These results suggest that studies on morphological variability may reflect adaptative and evolutionary processes and could subsequently be applied to biodiversity studies, in particular those dealing with nematode behaviour or activity. With regard to Mononchida, results suggest the need for further field research in order to establish (1) the limits of this intraspecific variability, (2) research on the genetic contribution and the role of environmental factors, (3) the significance of these morphologically different individuals from the functional and evolutionary aspect of the humus forms. Currently, work is being carried out to study the morphometry of these Mononchida species in plots with different humus forms as also the effect of calcic amendments on forest parcels which had an original moder humus form.

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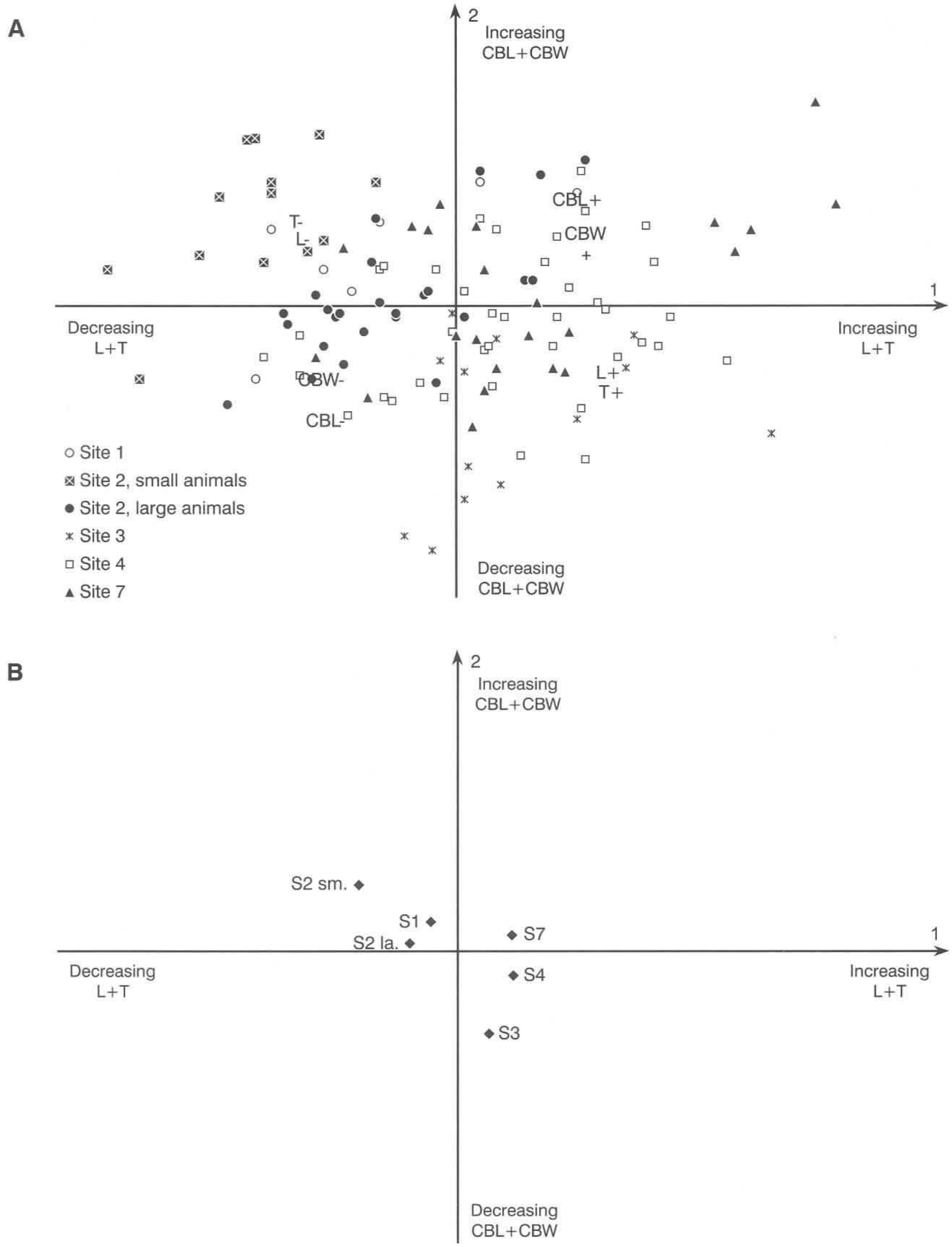

Figure 1. Factorial correspondence analysis (axes 1 and 2): Distribution of *Prionchulus punctatus* and variates according to the different sites (A); Average variate values for each site (B).

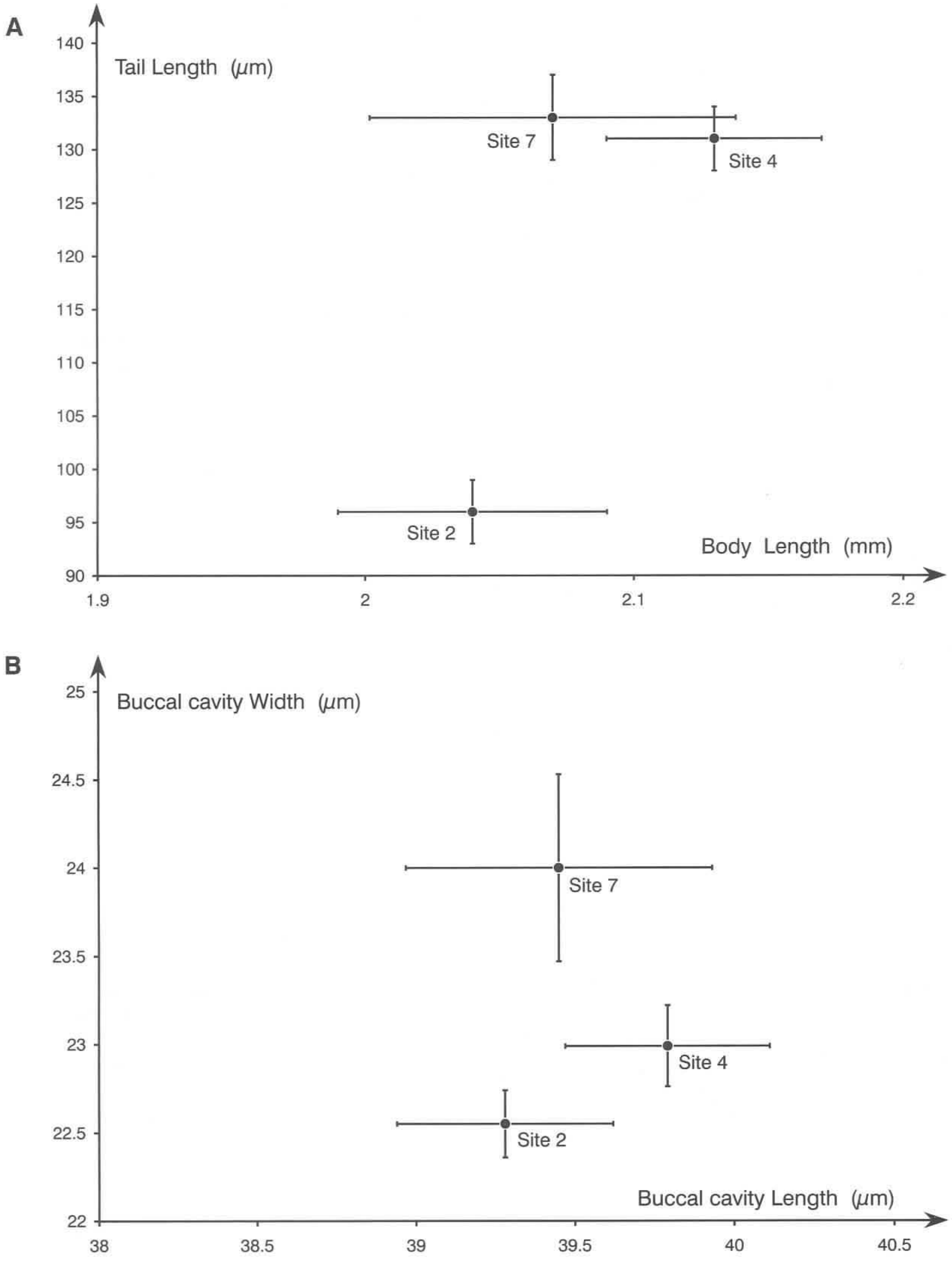

Figure 2. Mean (with confidence interval ± t $_{0.05}$ S_x) tail and body length (A) and buccal cavity length and buccal cavity width (B) of *Prionchulus punctatus* from sites 2 (combined small and large forms), 4 and 7, (sites 2, 4 and 7 only were taken into account because of the low number of individuals collected from the other two sites).

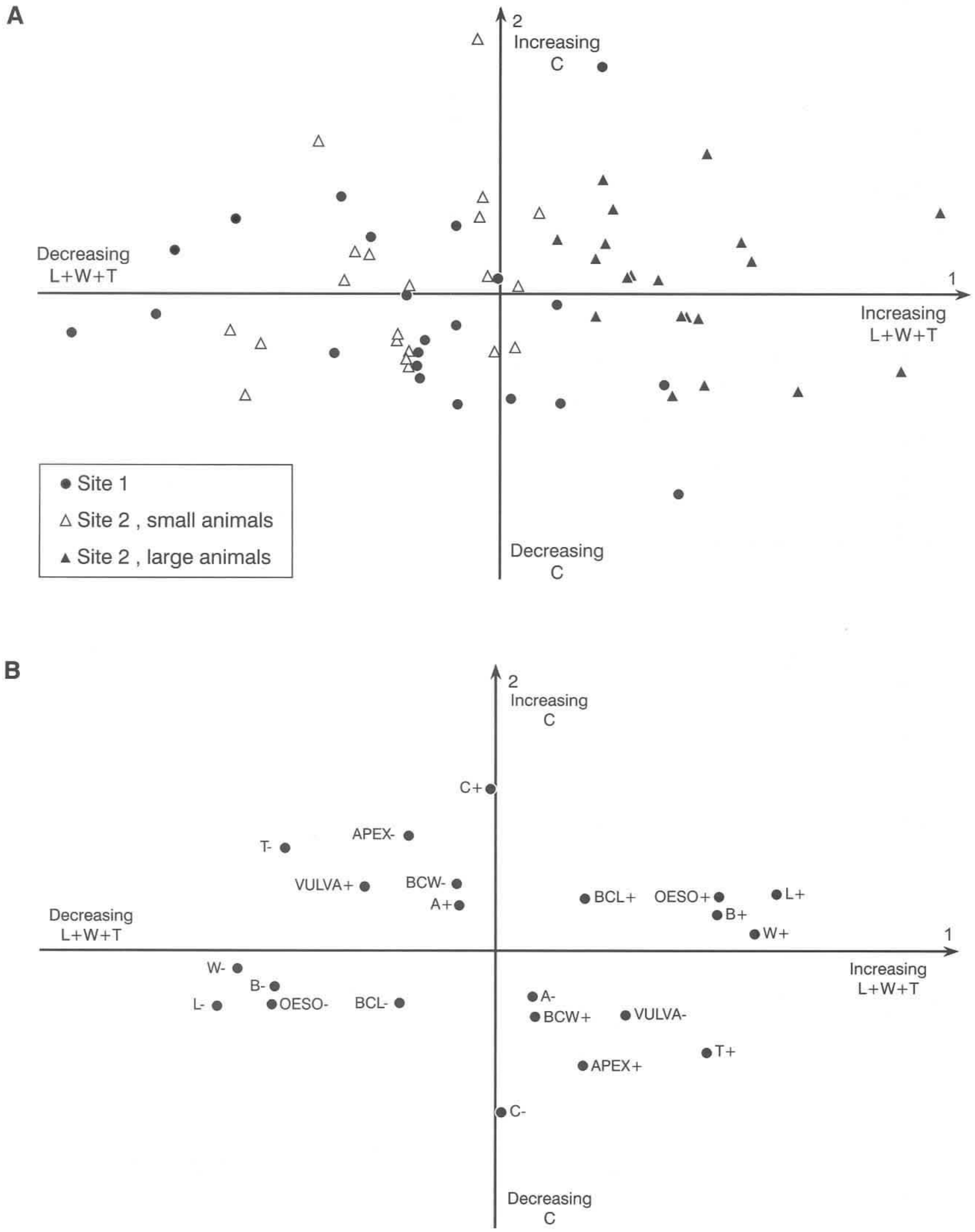

Figure 3. Factorial correspondence analysis (axes 1 and 2): Distribution of *Clarkus papillatus* (A) and variates (B) according to sites 1 and 2.

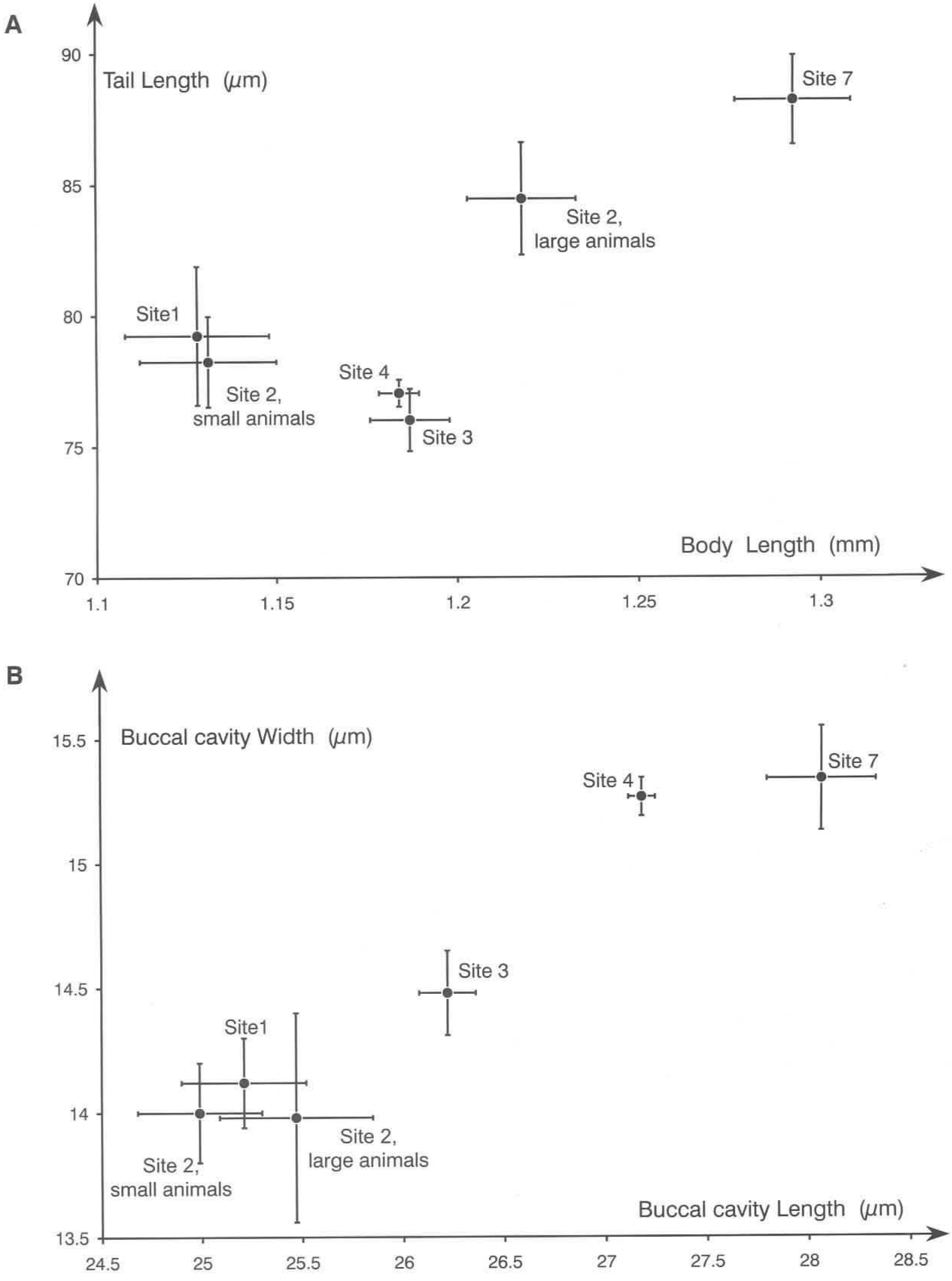

Figure 4. Mean (with confidence interval ± $t_{0.05} S_x$) tail and body length (A) and buccal cavity length and buccal cavity width (B) of *Clarkus papillatus* from sites 1, 2, 3, 4 and 7.

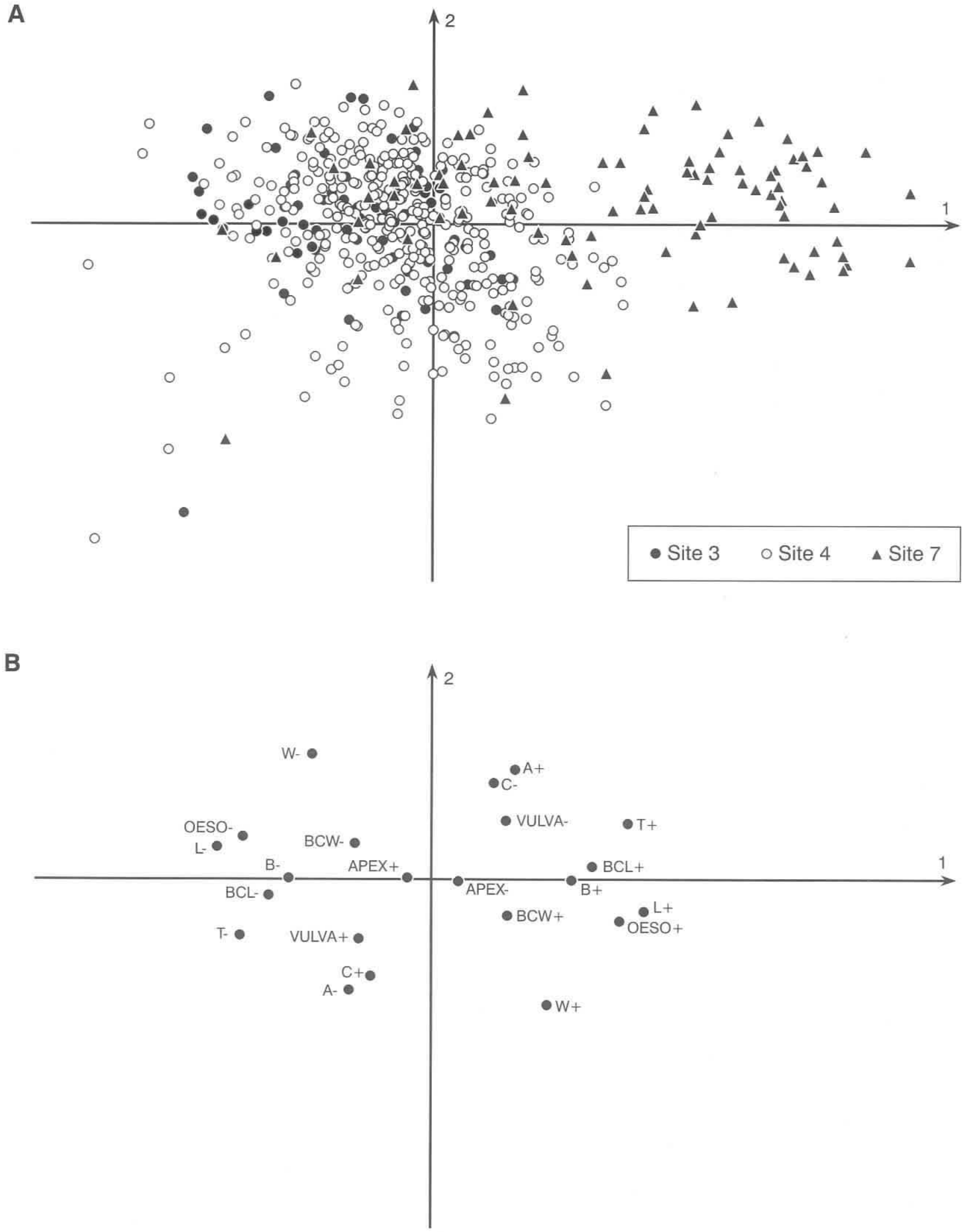

Figure 5. Factorial correspondence analysis (axes 1 and 2): Distribution of *Clarkus papillatus* (A) and variates (B) according to sites 3, 4 and 7.